

Floral resources impact longevity and oviposition rate of a parasitoid in the field

Jana C. Lee^{1*} and George E. Heimpel²

¹USDA ARS, Corvallis, OR 97330, USA; and ²Department of Entomology, University of Minnesota, St Paul, MN 55108, USA

Summary

1. The use of floral resource subsidies to improve herbivore suppression by parasitoids requires certain trophic interactions and physiological changes to occur. While the longevity and fecundity of parasitoids are positively affected by nectar subsidies in laboratory studies, the impacts of floral subsidies on the fecundity and longevity of freely foraging parasitoids have not been studied.

2. We studied the longevity and *per capita* fecundity of naturally occurring *Diadegma insulare* foraging in cabbage plots with and without borders of flowering buckwheat, *Fagopyrum esculentum*, as well as relationships between longevity, fecundity, sugar feeding and parasitism rates on larvae of the diamondback moth, *Plutella xylostella*.

3. Relative longevity was estimated by counting broken setae on the fringe of the forewing. Floral borders increased the longevity of males and females in adjacent cabbage plots.

4. The egg maturation rate of *D. insulare* was estimated by comparing egg loads of females collected early in the day with egg loads of females held without hosts in field cages throughout the day. Females in buckwheat cages matured 2·7 eggs per hour while females in control cages resorbed 0·27 eggs over the same time period.

5. The fecundity of females collected in the afternoon was estimated by comparing their actual egg load to the estimated egg load in the absence of oviposition for females in a given plot. Females foraging in buckwheat plots had marginally fewer eggs remaining in their ovaries, and laid marginally more eggs than females in control plots. Females from both treatments carried 30–60 eggs by the afternoon and therefore were time-limited rather than egg-limited.

6. Plots where a greater proportion of females had fed on sugar had longer-lived females. This suggests that feeding enhanced longevity of *D. insulare*. However, plots with longer-lived and more fecund females did not exhibit higher parasitism rates, although the power of these tests were low.

Key-words: *Diadegma insulare*, egg load, fecundity, nectar, wing wear

Introduction

The use of habitat management in conservation biological control provides opportunities to test hypotheses involving the impact of resource subsidies on community structure (Kean *et al.* 2003). The ‘parasitoid nectar provision hypothesis’ holds that biological control by parasitoids will be improved by nectar subsidies (Heimpel & Jervis 2005). The basic premise is that parasitoids tend to be sugar-limited in simplified agricultural habitats, and that by providing them with a nectar source, this limitation is alleviated, increasing their longevity, fecundity, and ability to suppress herbivorous pests. Some recent studies have documented parasitoids

ingesting sugars in the field from supplemental floral nectar or other sources (Casas *et al.* 2003; Wäckers & Steppuhn 2003; Heimpel *et al.* 2004; Lavandero *et al.* 2005; Winkler 2005; Lee, Andow & Heimpel 2006). Evidence that floral resources lead to increases in parasitism rates in agricultural settings is also mounting (English-Loeb *et al.* 2003; Tylianakis, Didham & Wratten 2004; Ellis *et al.* 2005; Lavandero *et al.* 2005), although this effect is by no means universal (Heimpel & Jervis 2005). What are largely missing are studies that mechanistically link sugar feeding to the population process of herbivore suppression. If supplemental nectar improves herbivore suppression by alleviating sugar limitation among parasitoids, we would expect parasitoid fecundity to increase in the presence of supplemental nectar. In this paper, we determine the effect of supplementary nectar on the fecundity and longevity of naturally foraging parasitoids.

*Correspondence author. E-mail: jana.lee@ars.usda.gov

The ways that common sugars or floral nectar improve parasitoid longevity and fecundity are widely documented in laboratory studies. A single sugar meal can reduce the risk of starvation by 73% (Siekmann, Tenhumberg & Keller 2001). Feeding may increase fecundity via several non-exclusive mechanisms. First, sugar feeding can affect egg load directly either by reducing the rate of egg resorption (Heimpel, Rosenheim & Kattari 1997), or by facilitating egg maturation (England & Evans 1997; Heimpel *et al.* 1997a; Olson & Andow 1998; Burger *et al.* 2004; Tylianakis *et al.* 2004). Feeding on sugar enables parasitoids to maintain high levels of glycogen and sugar reserves (Olson *et al.* 2000; Fadamiro & Heimpel 2001; Giron & Casas 2003; Lee, Heimpel & Leibe 2004; Fadamiro *et al.* 2005; Wyckhuys *et al.* 2008). Lipids are used in egg production (Ellers & van Alphen 1997; Casas *et al.* 2005), and ingesting sugars/nectar may reduce the rate of lipid decline (Ellers 1996; Lee *et al.* 2004; Casas *et al.* 2005) thereby possibly saving lipid reserves for egg production. Second, feeding can indirectly affect fecundity, through an increase in longevity allowing more time to oviposit (Berndt & Wratten 2005). Third, sugar feeding can provide energy required for efficient host foraging, thus increasing the oviposition rate (Schmale *et al.* 2001).

Much of our understanding of how parasitoids respond to resource subsidies comes from observable outcomes in the field such as parasitism rates and parasitoid abundance, and laboratory and field cage studies. Heimpel & Casas (2007) have recently stressed the need to compare parasitoid behaviour in the field and laboratory. While numerous studies support the view that parasitoids should live longer and have greater fecundity in the field with floral resources, other variables may compromise the benefits. The benefits of feeding may be negligible if factors such as high temperature (Dyer & Landis 1996; McDougall & Mills 1997; Chen, Onagbola & Fadamiro 2005) or heavy predation pressure in the field kills parasitoids at an age before starvation would be a major limiting factor (Rees & Onsager 1982; Heimpel, Rosenheim & Mangel 1997; Rosenheim 1998). Furthermore, floral habitats might attract hyperparasitoids or generalist predators that may attack nectar-feeding insects (Sholes 1984; Jervis 1990). Finally, other nectar or honeydew sugars may be available to parasitoids even in the absence of supplemental nectar sources, thus negating the assumption of sugar limitation (Casas *et al.* 2003; Wäckers & Steppuhn 2003; Heimpel & Jervis 2005; Lee *et al.* 2006a).

The impacts of floral resources on the longevity and fecundity of parasitoids foraging freely in the field have not yet been monitored. However, parasitoid behaviour can be studied in the field (reviewed by Heimpel & Casas 2007), and estimates of the realized fecundity of parasitoids in the field have also been obtained, but these can be complicated by the fact that many parasitoids mature eggs throughout the adult stage ('synovigeny'; Jervis *et al.* 2001). Casas *et al.* (2000) handled this problem by accounting for egg maturation rates of the synovigenic *A. melinus* as part of their estimation of egg laying (Casas *et al.* 2000).

In our studies, we used a wing wear index for a parasitoid (Lee, Leibe & Heimpel 2006), and methods pioneered by Casas *et al.* (2000) to determine the impact of floral resources on the longevity and *per capita* realized fecundity of a parasitoid in the field. We studied *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), a dominant native, synovigenic parasitoid of larvae of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) in the presence of annual flowering buckwheat *Fagopyrum esculentum* (Moench) (Polygonaceae) floral borders. Buckwheat has often been used in past studies of sugar supplementation (Heimpel & Jervis 2005), and has an open corolla that parasitoids can easily feed from.

Methods

The experiment was conducted in cabbage fields in the University of Minnesota Field Experiment Station in Rosemount, Minnesota, USA. We monitored *D. insulare*'s fecundity in 2002 and longevity in 2002–03 in 16 cabbage plots (12 m × 20 m) with or without buckwheat borders (four plots for each treatment per year). All plots were separated by at least 800 m to minimize parasitoid movement among plots (map in Lee & Heimpel 2005). Each plot was embedded in a separate soybean field since soybean is common in Midwest US landscapes and soybean nectar cannot be fed upon by common parasitoids of cabbage pests (Lee 2004). Cabbage (cv. 'Gourmet') seedlings were transplanted on 6 June 2002 and 5 June 2003. Plots consisted of 12 rows 20 m long, with c. 55 cabbage plants in each row, and with 100 cm between rows. Cabbage plots were planted in new sites each year, left untreated by chemicals with weeds removed by hand. Buckwheat strips (3 m wide) were planted along the 20 m borders on 11 June 2002, and 9 June 2003, and then planted along the 12 m borders on 3 July 2002 and 14 July 2003 to maintain a constant supply of blooming flowers throughout the summer.

LONGEVITY

To determine the impacts of floral nectar on longevity, the number of broken setae on the fringe of the forewing between the Rs and Cu vein was counted on field-collected *D. insulare*. The number of broken setae consistently increased linearly with age for *D. insulare* in several laboratory and field cage calibrations, demonstrating that the number of broken wing setae can estimate relative age (Lee *et al.* 2006b). *D. insulare* wasps foraging among cabbage plants were captured with aspirators made of plastic tubing connected to a bluntly cut 1 mL pipette tip with fine mesh glued to the cut end. Aspirated wasps were gently expelled into 1.5 mL microcentrifuge tubes with mesh bottoms. Wasps were collected between 9 am and 3 pm from 30 July to 2 September 2002 and 24 July–21 August 2003 when they were abundant along the cabbage rows, and buckwheat plants were in bloom. In 2002, fecundity of field-collected wasps was simultaneously being assessed, which required a full day of sampling an individual plot on at least three given days (dates and number captured in Table 1). In 2003, wasps were collected on six different days per plot. *Diadegma insulare* captured on all dates within a plot were pooled together by sex, and the effects of treatment, year and treatment × year on the number of broken setae per wing were tested using an ANOVA, with plot as the experimental unit and the number of wasps per plot as subsamples (SAS 1995). The total number of fringe wing setae between the Rs and Cu veins ranged

Table 1. ANOVA for treatment, year and treatment–year interactions on the number of the broken wing setae in *D. insulare*, and effect of treatment on the ovarian egg load in the morning and afternoon, egg maturation rates, and number of eggs laid by *D. insulare* females

		Effect	d.f.	F	P
Broken fringe wing setae ^a	Females years 1–2 ^b	treatment	1,12	16.4	0.0016
		year	1,12	2.2	0.16
		treatment × year	1,12	0.05	0.83
	Males years 1–2 ^c	treatment	1,12	13.4	0.0033
		year	1,12	4.2	0.064
		treatment × year	1,12	5.0	0.045
Initial egg load	Morning females year 1 ^d	treatment	1,6	11.9	0.014
Remaining egg load	Afternoon females year 1 ^e	treatment	1,6	5.7	0.055
Eggs laid per hour	Afternoon females year 1	treatment	1,6	4.7	0.072

^aSampling dates in year 1: buckwheat (plot one) 7, 15, 27, and 29 August 2002 (two) 6, 9, 16, and 30 August (three) 2, 11, and 20 August (four) 30 July, 13 and 20 August, and control (plot one) 6, 14, and 27 August (two) 23, and 28 August, 2 September (three) 30 July, 11, 13, and 22 August (four) 8, 20, and 24 August. Sampling in year 2 for broken wing hair on 25 and 31 July, 1 and 7 August, 2003 in all eight plots, 14 and 21 August in two buckwheat and two control plots, and 12 and 18 August in the other four plots.

^bNumber of female wasps per plot (subsamples), buckwheat-81, 114, 63, 78 in year 1; 39, 23, 39, 32 in year 2; control-72, 127, 95, 75 in year 1; 23, 32, 26, 50 in year 2.

^cNumber of male wasps per plot, buckwheat-115, 125, 124, 103 in year 1; 60, 69, 61, 69 in year 2; control-69, 24, 131, 51 in year 1; 77, 67, 71, 57 in year 2.

^dNumber of subsamples, buckwheat-13, 16, 12, 12; control-12, 30, 13, and 15.

^eNumber of subsamples, buckwheat-32, 38, 24, 35; control-21, 43, 39, 31.

between 139 and 144, and the maximum number of broken setae on an individual wasp was 38. Assumptions of ANOVA were met with respect to the treatments and broken fringe wing setae.

FECUNDITY

To assess fecundity in 2002, *D. insulare* foraging among cabbage plants were collected from 9 am to 3 pm, when females are most active (Idris & Grafius 1998) and readily captured via aspiration. Sampling was conducted as described in the longevity study in 2002. Wasps were frozen in 1.5 mL microcentrifuge tubes with the time recorded. Since *D. insulare* are synovigenic, counting egg loads of females would not directly reveal how many eggs were laid. We used methods similar to Casas *et al.* (2000) to estimate the number of eggs laid by synovigenic parasitoids. Half of the females collected between 9 and 10 am were frozen immediately, and the other half were released into a 30.5 × 30.5 × 61 (l × w × h) cm white plastic mesh cage (two BioQuip® 'Bug dorms' linked together; BioQuip® Rancho Dominguez, CA, USA) placed in the same field. Clusters of buckwheat or soybean foliage, depending on the treatment, were inserted into the cage through a sleeve while the plants remained rooted in the soil. This allowed females to mature eggs with food and shelter resources available in the plot, while not having access to hosts. Caged wasps were frozen at 3 pm. To estimate the number of eggs available at the start of the day, 'morning' females frozen at 9–10 am were dissected and the eggs in their ovaries counted. To estimate the number of eggs matured over the 6-h study period, eggs were counted in 'caged' females deprived of hosts.

Egg load data from the 'morning' and 'caged' wasps were used to estimate fecundity with egg maturation rates calibrated separately for each plot. The egg loads of 'morning' and 'caged' females were graphed against time with a linear regression to generate estimates of hypothetical egg loads in the absence of oviposition over the 6-h period (Fig. 1 illustrates how this calculation was done for one of the plots). Females collected between 1 and 3 pm were designated 'afternoon'. Although *D. insulare* females continue flying after

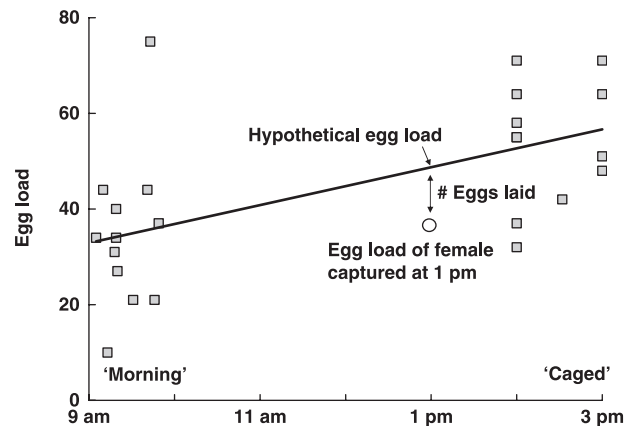


Fig. 1. Linear egg load estimation for *D. insulare* females in one representative buckwheat plot to illustrate the method for estimating the oviposition rate. Points indicate egg loads of females collected during the first hour (09.00–10.00 h) that were either frozen or caged and allowed to mature eggs ('morning' $n = 12$, 'caged' $n = 12$). The estimated number of eggs laid by a collected female is the difference between the hypothetical egg load in the absence of hosts and the egg load of collected female at the given time.

3 pm, their flight activity peaks at noon and then declines (Idris & Grafius 1998), so that fewer wasps were active after 3 pm. The egg load of each 'afternoon' female was compared to the hypothetical egg load generated by the host-deprived caged wasps to estimate how many eggs had been laid (Fig. 1). Egg laying was estimated on a per-hour basis since wasps were collected between 1 and 3 pm. All 'afternoon' females were pooled together by plot and tested for treatment effects in an ANOVA. While egg load can vary by female size, females had similar wing lengths of 3.28 ± 0.018 mm (mean \pm SEM) in buckwheat, and 3.29 ± 0.017 in control treatments, so no adjustments were made for size.

RELATIONSHIPS BETWEEN FEEDING AND PARASITISM RATES

The effects of longevity (broken wing setae), fecundity (eggs laid per hour), the proportion of sugar-fed wasps, and the probability of nectar feeding, on parasitism rates of *P. xylostella* were examined. Sugar and nectar feeding of wasps were determined by Lee *et al.* (2006a), where sugar feeding was determined using biochemical analysis to detect fructose. Newly emerged and starved *D. insulare* have less than 1 µg of fructose Lee *et al.* (2004). The probability of nectar feeding (as opposed to honeydew feeding) for the subset of wasps that fed on sugars was determined using methods described by Lee *et al.* (2006a). Parasitism on *P. xylostella* was assessed in the same experimental plots by rearing all larvae collected from 5–10 random cabbage plants per plot each week (Lee & Heimpel 2005). Regression models were used to investigate the effects of treatment, and proportion of wasps sugar-feeding or probability of nectar feeding (x-variables) on the number of broken wing fringe setae, or the estimated number of eggs laid per hour. In separate models, the effects of treatment, broken wing fringe setae or eggs laid per hour on the proportion of diamondback larvae parasitized were investigated. *A priori* power tests determined the effect size ($f^2 = r^2/(1 - r^2)$) necessary for a significant regression with G*Power 3 (Faul *et al.* 2007) given: Power = 0.80, 0.95, sample size (plots) = 8, 16, and $\alpha = 0.05$.

Results

LONGEVITY

Both female and male *D. insulare* collected from buckwheat plots had significantly more broken wing setae than those collected from control plots (Table 1; Fig. 2). For males, the treatment-year interaction was significant, reflecting the fact that in year 1, males from buckwheat had more broken setae than those from control plots, and in year 2, males from both treatments had similar numbers of broken setae.

FECUNDITY

'Morning' females collected from buckwheat plots had significantly lower egg loads than those collected from

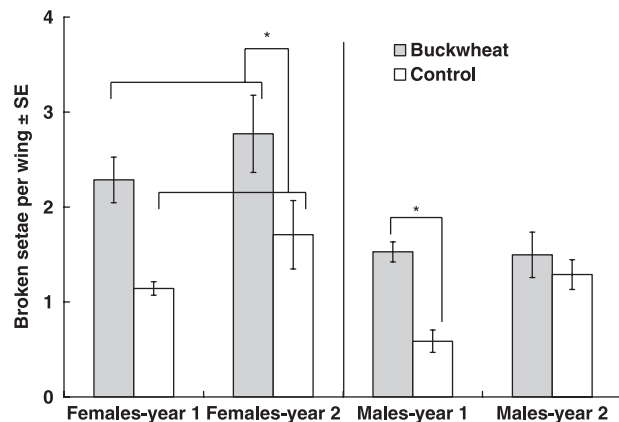


Fig. 2. Number of broken fringe setae per wing for female and male *D. insulare* from buckwheat and control treatments. Asterisk indicates significant difference, $\alpha < 0.05$.

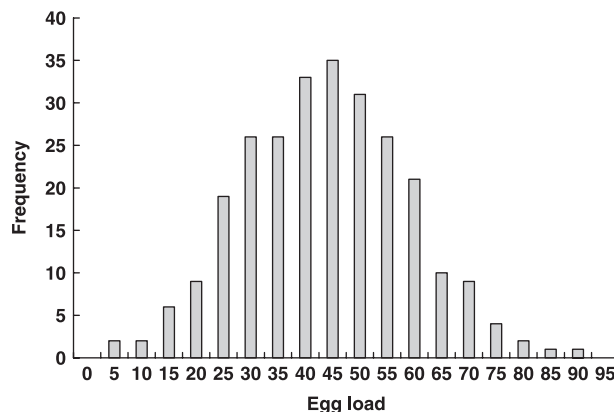


Fig. 3. Egg load distribution of 263 'afternoon' *D. insulare* females collected from the field from 13.00–15.00 h.

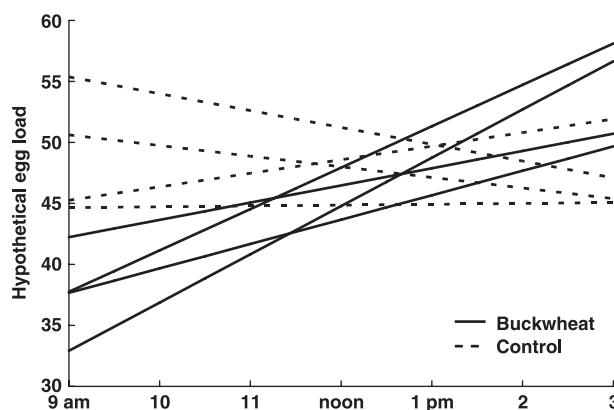


Fig. 4. Egg maturation curves calculated from 'morning' and 'caged' *D. insulare* females in four buckwheat and four control plots. Equations and sample sizes listed in Table 2.

control plots (mean \pm SE) 38.9 ± 1.76 and 48.9 ± 2.31 eggs, respectively (Table 1). 'Afternoon' females collected in the field had egg loads ranging from 6 to 90, and the 25–75% quantile range for all females was 35–57 eggs (Fig. 3). Egg loads of 'afternoon' females from buckwheat plots were marginally significantly lower than those of females from control plots, 44.3 ± 0.53 and 46.8 ± 0.87 , respectively (Table 1). When calculating egg maturation rates using 'morning' and 'caged' females, egg loads increased by 2.69 ± 0.592 eggs per hour with respect to wasps caged with buckwheat plants, and decreased by 0.268 ± 0.549 eggs per hour with respect to wasps caged with soybean in control plots (Fig. 4). Two of the four slopes of hypothetical egg load from buckwheat plots were significantly greater than zero, while none of the slopes from the control plots were significantly different from zero (Table 2). A comparison of slopes suggests that egg maturation was greater in buckwheat than control plots (Table 2; Fig. 4); the average slope was 0.0457 ± 0.0105 for buckwheat, and -0.00446 ± 0.00915 for control plots. Using this maturation estimate, treatment had a marginally significant effect on eggs laid by 'afternoon' females (Table 1). Females laid 1.38 ± 0.33 eggs per hour in cabbage plots bordered by buckwheat and 0.27 ± 0.43 eggs per hour in control plots.

Table 2. Egg maturation calibration lines for 'morning' and 'caged' *D. insulare* females, and comparisons of egg maturation rates by treatment

Plot	Eggs = intercept + slope (min) min = 0 at 09.00 h	Linear regression			
		d.f.	F	P	r ²
Buckwheat	$y = 32.92 + 0.06594x$	1,22	11.4	0.0027	0.312
Buckwheat	$y = 37.67 + 0.03333x$	1,22	2.3	0.14	
Buckwheat	$y = 37.75 + 0.05655x$	1,18	7.7	0.012	0.261
Buckwheat	$y = 42.23 + 0.02356x$	1,28	1.1	0.30	
Control	$y = 44.66 + 0.00114x$	1,56	0.0074	0.93	
Control	$y = 45.25 + 0.01852x$	1,21	0.54	0.47	
Control	$y = 50.62 - 0.01451x$	1,26	0.46	0.50	
Control	$y = 55.37 - 0.02299x$	1,22	1.3	0.27	
Effect of treatment on				ANOVA	
Egg maturation slopes		1,6	13.0	0.011	

Number of wasps per plot = 24, 24, 20, 30, 58, 23, 28, and 24, respectively.

RELATIONSHIPS BETWEEN FEEDING AND PARASITISM RATES

The first set of regressions tested whether treatment and feeding status could account for some of the variation in longevity and fecundity of *D. insulare* in the field. The proportion of females that were sugar-fed significantly increased with broken wing setae at the per-plot level (Table 3, Fig. 5a). For males, plots where more males had fed on sugar or had a higher probability of nectar feeding, likewise had males with marginally more broken wing setae (Table 3). There was no relationship between the proportion of sugar-fed females nor the probability of nectar feeding on the number of eggs laid per hour in the eight plots. Lastly, the number of broken wing setae and eggs laid did not affect parasitism rates on *P. xylostella* larvae (Table 3, Fig. 5b). However, the effect size needed for these tests was high due to the low sample size of 8 or 16 plots. The criteria r^2 was 0.43 or higher, and only predictors such as proportion sugar-fed and probability of nectar feeding on broken wing setae had an r^2 above 0.4 (Table 3).

Discussion

Buckwheat floral borders had a positive impact on the longevity of *D. insulare* females and males foraging in the field, as determined by broken wing setae counts. Floral habitat appeared to enhance fecundity, as 'afternoon' females from buckwheat treatments had marginally lower ovarian egg loads toward the end of the foraging period, and laid marginally more eggs per hour than females from controls. Also, egg loads at the beginning of the foraging day were significantly lower among females from buckwheat than control plots, suggesting that more eggs were laid the previous day, that females were not maturing a compensatory amount of eggs overnight, and that females tend to remain in the same patch for two consecutive days. Moreover, plots where a greater proportion of wasps had fed on sugar, or where wasps had higher probabilities of nectar feeding, likewise had longer-lived wasps. This is, to our knowledge, the first demonstration that floral habitat can influence the longevity and fecundity of naturally

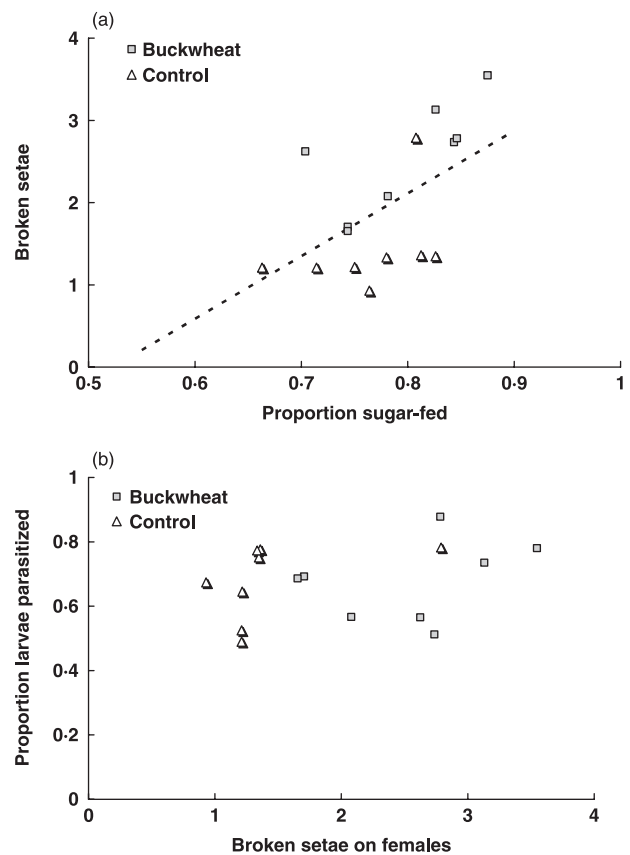


Fig. 5. Relationships between (a) the proportion of females that have fed on sugar and the number of broken wing setae (linear regression d.f. = 1,14, $F = 7.5$, $P = 0.016$, $y = -3.98 + 7.62x$, $r^2 = 0.30$), and (b) the number of broken wing setae of females and parasitism rates of diamondback larvae.

occurring parasitoids in the field, and that ingestion of nectar or other sources correlates with longevity, corroborating laboratory and field-cage studies with *D. insulare* (Idris & Grafius 1995; Johanowicz & Mitchell 2000; Gouridine *et al.* 2003; Lee *et al.* 2004) and *D. semiclausum* (Winkler *et al.* 2005).

While wasps from buckwheat treatments broke about one more seta than wasps from controls, the actual age difference is

Table 3. Regression models testing relationships among field-collected *D. insulare*: the effects of treatment and feeding on the number of broken wing fringe setae, or on the number of eggs laid per hour; and effects of treatment, and broken fringe wing setae or number of eggs laid per hour on larval parasitism rates. *A priori* power tests determining the effect size ($r^2/(1-r^2)$) necessary for given power levels and sample sizes

Response (y-variable)	Treatment (x-variable)			Main x-variable of interest	d.f.	F	P	r^2	Effect size expressed as r^2	
	d.f.	F	P						power = 0.80	power = 0.95
Broken wing setae	1,13	16.0	0.0015	Prop. sugar-fed	1,13	5.0	0.042	0.674	0.434	0.552
Broken wing setae	1,13	12.7	0.0034	Prob. (nectar feeding)	1,13	0.27	0.61	0.557	0.434	0.552
Broken wing setae	1,13	5.0	0.044	Prop. sugar-fed	1,13	3.8	0.073	0.478	0.434	0.552
Broken wing setae	1,13	16.0	0.015	Prob. (nectar feeding)	1,13	4.38	0.057	0.495	0.434	0.552
Eggs laid per hour	1,5	4.9	0.072	Prop. sugar-fed	1,5	0.76	0.42	0.322	0.700	0.795
Eggs laid per hour	1,5	1.8	0.24	Prob. (nectar feeding)	1,5	0.13	0.73	0.238	0.700	0.795
Prop. Parasitism	1,13	0.31	0.59	Broken wing setae	1,13	0.50	0.49	0.380	0.434	0.552
Prop. Parasitism	1,5	0.12	0.74	Eggs laid per hour	1,5	0.44	0.54	0.283	0.700	0.795

unknown. Overall, field-collected wasps broke very few setae, often less than 3 per wing, whereas wasps kept in field cages broke 10 setae per day (Lee *et al.* 2006b). This could suggest either that *D. insulare* in the field are very short-lived or that wasps break setae much more slowly when foraging freely than in closed environments. Using broken wing setae as a relative age estimate assumes that wasps were breaking setae similarly per unit time in both treatments. While setae breakage rates can vary greatly by environment (Lee *et al.* 2006b), both treatments were similar in structure with cabbage rows and dense vegetation surrounding it. In the laboratory, *D. insulare* caged with buckwheat, soybean and honey broke setae at a slower rate than those that were caged with only soybean plants and honey (Lee *et al.* 2006b). Thus, the greater number of broken setae of *D. insulare* from buckwheat treatment probably reflects greater age of wasps in buckwheat vs. control plots.

In the fecundity study, when comparing egg loads of 'morning' and 'caged' females, egg maturation was higher with access to floral nectar than soybean plants, although only marginally significant. *Diadegma insulare* caged without buckwheat flowers resorbed eggs or matured eggs more slowly than wasps caged with nectar. This may have resulted from wasps not obtaining adequate amounts of sugar in the soybean cage. While soybean aphid honeydew may have been present in the cages, we have shown previously that this sugar source has a lower nutritional value than buckwheat nectar for *D. insulare* (Lee *et al.* 2004). Other parasitoids have greater egg loads when given sugar/nectar than when starved (Hagley & Barber 1992; England & Evans 1997; Tylianakis *et al.* 2004). *Aphytis melinus* resorbed nine eggs when starved over a 36 h-period whereas honey-fed females did not resorb any eggs over the same time period (Heimpel *et al.* 1997a). In our study, females in buckwheat plots laid 1.4 eggs per hour while females in control plots laid 0.3 eggs per hour. A difference of 1.1 more eggs laid per hour represents a 4.6-fold increase in fecundity over the time course of our observations. This increase in egg laying by *D. insulare* in buckwheat plots might be explained by greater egg maturation rates that lead to greater search intensity and successful host encounters (Minkenberg, Tatar & Rosenheim 1992; Heimpel & Rosenheim 1998; Mangel & Heimpel 1998). However, females collected from both treatments in the afternoon often had 30–60 eggs remaining in their ovaries, suggesting that *D. insulare* in our fields were probably more time-limited than egg-limited. This would argue against reduced foraging at relatively low egg loads, although egg loads do not need to be near zero to alter oviposition strategies (e.g. Rosenheim & Rosen 1991; Collier, Murdoch & Nisbet 1994; Fletcher, Hughes & Harvey 1994; Hughes, Harvey & Hubbard 1994; Heimpel & Rosenheim 1995; Michaud & Mackauer 1995).

Neither longevity nor fecundity of *D. insulare* females within a plot accounted for variation of parasitism rates of *P. xylostella* larvae. Parasitism rates in those same plots in year 2002–2003 were also not affected by the floral borders (Lee & Heimpel 2005). Since females from buckwheat plots

had higher longevity and possibly fecundity than females from controls, and females had an abundance of eggs, the failure of floral supplementation to increase parasitism rates was unexpected. This lack of an effect could be due to the high effect size and r^2 needed for a significant regression with sample sizes of 8 or 16 plots, or it could indicate that some assumptions about *D. insulare* behaviour within diversified habitats are unmet. First, feeding may provide *D. insulare* with ample carbohydrate reserves and induce them to disperse to other host sites. For example, *D. insulare* might disperse to other host patches to avoid inbreeding depression (Butcher, Whitefield & Hubbard 2000). Or, parasitoids might leave plots when hosts are no longer found at a certain rate, as predicted by the marginal value theorem (Charnov 1976). More specifically, the host-encounter-rate threshold required for leaving a patch may be lower for well-fed wasps than starving wasps because the fed wasps have adequate energy reserves for flight. Second, host searching might decrease when the habitat is diversified, as found with *D. semiclausum* in monoculture vs. intercropped brassicas (Gols *et al.* 2005). Thus, the time spent by parasitoids within buckwheat vegetation may compete with time spent searching for hosts (Sirot & Bernstein 1996). Third, although fed *D. insulare* may live longer, they may spend additional time in other activities such as grooming or resting, detracting from host searching activity. In the laboratory, sugar-fed *D. insulare* were less likely to walk/fly into a small host patch than were starved wasps (Lee & Heimpel 2007). Although actively flying wasps from buckwheat treatments might have oviposited more during a foraging bout, more wasps might be inactive in buckwheat than control plots and have remained unmonitored by our collection techniques. Thus, females could be more efficient for short durations in buckwheat treatments but have similar lifetime fecundities to those of females in control treatments. Due to the difficulty of determining oviposition rates among synovigenic parasitoids, short-term oviposition was estimated but lifetime fecundity remains unknown.

Although floral resources improved the longevity and possibly short-term fecundity of *D. insulare* foraging in adjacent cabbage fields, it did not clearly lead to increased overall parasitism rates. Likewise, other floral habitat manipulations in the field have not consistently improved biological control (reviewed by Heimpel & Jervis 2005). These unexpected results emphasize the need to better understand parasitoid behaviour and lifetime fecundity in the presence of floral nectar sources and to determine whether factors such as dispersal or searching rates differ between sugar-fed and starved parasitoids.

Acknowledgements

We thank Kathy Kurtz, Gregory Miller, Carmen Gavin, and Matt Heineke for countless hours catching wasps in the field. We thank Kimon and Jim Karels at Rosemount UMORE for experimental set-up and maintenance. This research was funded in part by USDA NRI Grant no. 9802906, a USDA North Central Regional IPM grant to G.E.H., Louise T. Dosdall and Doctoral Dissertation Fellowship to J.C.L., and the University of Minnesota Agricultural Experiment Station.

References

- Berndt, L.A. & Wratten, S.E. (2005) Effects of alyssum flowers on the longevity, fecundity, and sex ratio of the leafroller parasitoid *Dolichogenideia tasmanica*. *Biological Control*, **32**, 65–69.
- Burger, J.M.S., Reijnen, T.M., van Lenteren, J.C. & Vet, L.E.M. (2004) Host feeding in insect parasitoids: why destructively feed upon a host that excretes an alternative? *Entomologia Experimentalis et Applicata*, **112**, 207–215.
- Butcher, Royal, D.J., Whitefield, W.G.F. & Hubbard, S.F. (2000) Complementary sex determination in the genus *Diadegma* (Hymenoptera: Ichneumonidae). *Journal of Evolutionary Biology*, **13**, 593–606.
- Casas, J., Driessen, G., Mandon, N., Wielaard, S., Desouhant, E., Van Alphen, J., Lapchi, L., Rivero, A., Christides, J.P. & Bernstein, C. (2003) Energy dynamics in a parasitoid foraging in the wild. *Journal of Animal Ecology*, **72**, 691–697.
- Casas, J., Nisbet, Royal M., Swarbrick, S. & Murdoch, W.W. (2000) Eggload dynamics and oviposition rate in a wild population of a parasitic wasp. *Journal of Animal Ecology*, **69**, 185–193.
- Casas, J., Pincebourde, S., Mandon, N., Vannier, F., Poujol, Royal, G. & Giron, D. (2005) Lifetime nutrient dynamics reveal simultaneous capital and income breeding in a parasitoid. *Ecology*, **86**, 545–554.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.
- Chen, L., Onagbola, E.O. & Fadamiro, H.Y. (2005) Effects of temperature, sugar availability, gender, mating, and size on the longevity of phorid fly *Pseudacteon tricuspis* (Diptera: Phoridae). *Environmental Entomology*, **34**, 246–255.
- Collier, T. Royal., Murdoch, W.W. & Nisbet, Royal M. (1994) Egg load and the decision to host-feed in the parasitoid *Aphytis melinus*. *Journal of Animal Ecology*, **63**, 299–306.
- Dyer, L.E. & Landis, D.A. (1996) Effects of habitat, temperature, and sugar availability on longevity of *Eriborus terebrans* (Hymenoptera: Ichneumonidae). *Environmental Entomology*, **25**, 1192–1201.
- Ellers, J. (1996) Fat and eggs: an alternative method to measure the trade-off between survival and reproduction in insect parasitoids. *Netherlands Journal of Zoology*, **46**, 227–235.
- Ellers, J. & van Alphen, J.H.M. (1997) Life history evolution in *Asobara tabida*: plasticity in allocation of fat reserves to survival and reproduction. *Journal of Evolutionary Biology*, **10**, 771–785.
- Ellis, J.A., Walter, A.D., Tooker, J.F., Ginzler, M.D., Reagel, P.F., Lacey, E.S., Bennet, A.B., Grossman, E.M. & Hanks, L.M. (2005) Conservation biological control in urban landscapes: manipulating parasitoids of bagworm (Lepidoptera: Psychidae) with flowering forbs. *Biological Control*, **34**, 99–107.
- England, S. & Evans, E.W. (1997) Effects of pea aphid (Homoptera: Aphididae) honeydew on longevity and fecundity of the alfalfa weevil (Coleoptera: Curculionidae) parasitoid *Bathypsectes curculionis* (Hymenoptera: Ichneumonidae). *Environmental Entomology*, **26**, 1437–1441.
- English-Loeb, G., Rhainds, M., Martinson, T. & Ugine, T. (2003) Influence of flowering cover crops on *Anagrus* parasitoids (Hymenoptera: Mymaridae) and *Erythroneura* leafhoppers (Homoptera: Cicadellidae) in New York vineyards. *Agricultural and Forest Entomology*, **5**, 173–181.
- Fadamiro, H.Y., Chen, L., Onagbola, E.O. & Graham, L.F. (2005) Lifespan and patterns of accumulation and mobilization of nutrients in the sugar-fed phorid fly, *Pseudacteon tricuspis*. *Physiological Entomology*, **30**, 212–224.
- Fadamiro, H.Y. & Heimpel, G.E. (2001) Effects of partial sugar deprivation on lifespan and carbohydrate mobilization in the parasitoid *Macrocentrus grandii* (Hymenoptera: Braconidae). *Annals of the Entomological Society of America*, **94**, 909–916.
- Faul, F., Erdfelder, E., Lang, A.-G. & Buchner, A. (2007) G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, **39**, 175–191.
- Fletcher, J.P., Hughes, J.P. & Harvey, I.F. (1994) Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. *Proceedings of the Royal Society of London, B*, **258**, 163–167.
- Giron, D. & Casas, J. (2003) Lipogenesis in an adult parasitic wasp. *Journal of Insect Physiology*, **49**, 141–147.
- Gols, Royal., Bukovinsky, Royal., Hemerik, L., Harvey, J.A., van Lenteren, J.C. & Vet, L.E.M. (2005) Reduced foraging efficiency of a parasitoid under habitat complexity: implications for population stability and species co-existence. *Journal of Animal Ecology*, **74**, 1059–1068.
- Gourdine, J.S., McCutcheon, G.S., Simmons, A.M. & Leibe, G.L. (2003) Kale floral nectar and honey as food sources for enhancing longevity and parasitism of *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of the Diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Journal of Agricultural and Urban Entomology*, **20**, 1–6.

- Hagley, A.C. & Barber, D. Royal (1992) Effect of food sources on the longevity and fecundity of *Pholetesor ornigis* (Weed) (Hymenoptera: Braconidae). *Canadian Entomologist*, **124**, 341–346.
- Heimpel, G.E. & Casas, J. (2007) Parasitoid foraging and oviposition behaviour in the field. *Behavioural Ecology of Insect Parasitoids* (eds E. Wajnberg, C. Bernstein & J.J.M. Van Alphen), pp. 51–70. Blackwell Publishing, Oxford, UK.
- Heimpel, G.E. & Jervis, M.A. (2005) Does floral nectar improve biological control by parasitoids? *Plant-Provided Food and Plant-Carnivore Mutualism* (eds F. Waeckers, P. van Rijn & J. Bruin), pp. 267–304. Cambridge University Press, Cambridge, UK.
- Heimpel, G.E., Lee, J.C., Wu, Z., Weiser, L., Wäckers, F. & Jervis, M.A. (2004) Gut sugar analysis in field-caught parasitoids: adapting methods originally developed for biting flies. *International Journal of Pest Management*, **50**, 193–198.
- Heimpel, G.E. & Rosenheim, J.A. (1995) Dynamic host feeding by the parasitoid *Aphytis melinus*: the balance between current and future reproduction. *Journal of Animal Ecology*, **64**, 153–167.
- Heimpel, G.E. & Rosenheim, J.A. (1998) Egg limitation in parasitoids: a review of the evidence and a case study. *Biological Control*, **11**, 160–168.
- Heimpel, G.E., Rosenheim, J.A. & Kattari, D. (1997a) Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus*. *Entomologia Experimentalis et Applicata*, **83**, 305–315.
- Heimpel, G.E., Rosenheim, J.A. & Mangel, M.A. (1997b) Predation on adult *Aphytis* parasitoids in the field. *Oecologia*, **110**, 346–352.
- Hughes, J.P., Harvey, I.F. & Hubbard, S.F. (1994) Host-searching behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): interference – the effect of mature egg load and prior behavior. *Journal of Insect Behavior*, **7**, 433–454.
- Idris, A.B. & Grafius, E. (1995) Wildflowers as nectar sources for *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). *Environmental Entomology*, **24**, 1726–1735.
- Idris, A.B. & Grafius, E. (1998) Diurnal flight activity of *Diadegma insulare* (Hymenoptera: Ichneumonidae) a parasitoid of the diamondback moth (Lepidoptera: Plutellidae) in the field. *Environmental Entomology*, **27**, 406–414.
- Jervis, M.A. (1990) Predation of *Lissonota coracinus* (Gmelin) (Hymenoptera: Ichneumonidae) by *Dolichonabes limbatus* (Dahlbom) (Hemiptera: Nabidae). *Entomologist's Gazette*, **41**, 231–233.
- Jervis, M.A., Heimpel, G.E., Ferns, P.N., Harvey, J.A. & Kidd, N.A.C. (2001) Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *Journal of Animal Ecology*, **70**, 442–458.
- Johanowicz, D.L. & Mitchell, E. Royal (2000) Effects of sweet alyssum flowers on the longevity of the parasitoid wasps *Cotesia marginiventris* (Hymenoptera: Braconidae) and *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Florida Entomologist*, **83**, 41–47.
- Kean, J., Wratten, S., Tylanakis, J. & Barlow, N. (2003) The population consequences of natural enemy enhancement, and implications for conservation biological control. *Ecology Letters*, **6**, 604–612.
- Lavandero, B., Wratten, S., Shishebor, P. & Worner, S. (2005) Enhancing the effectiveness of the parasitoid *Diadegma semiclausum* (Helen): movement after use of nectar in the field. *Biological Control*, **34**, 152–158.
- Lee, J.C. (2004) *Diversifying Agroecosystems with Floral Habitat to Improve Biological Control*. PhD Thesis, University of Minnesota, St. Paul.
- Lee, J.C., Andow, D.A. & Heimpel, G.E. (2006a) Influence of floral resources on sugar feeding and nutrient dynamics of a parasitoid in the field. *Ecological Entomology*, **5**, 143–178.
- Lee, J.C. & Heimpel, G.E. (2005) Impact of flowering buckwheat on lepidopteran cabbage pests and their parasitoids at two spatial scales. *Biological Control*, **34**, 290–301.
- Lee, J.C. & Heimpel, G.E. (2007) Sugar feeding may reduce short-term activity of a parasitoid wasp. *Physiological Entomology*, **32**, 99–103.
- Lee, J.C., Heimpel, G.E. & Leibe, G.L. (2004) Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomologia Experimentalis et Applicata*, **111**, 189–199.
- Lee, J.C., Leibe, G.L. & Heimpel, G.E. (2006b) Broken wing setae as a relative estimate of parasitoid age. *Entomologia Experimentalis et Applicata*, **121**, 87–92.
- Mangel, M. & Heimpel, G.E. (1998) Reproductive senescence and dynamic oviposition behaviour in insects. *Evolutionary Ecology*, **12**, 871–879.
- McDougall, S.J. & Mills, N.J. (1997) The influence of hosts, temperature and food sources on the longevity of *Trichogramma platneri*. *Entomologia Experimentalis et Applicata*, **83**, 195–203.
- Michaud, J.P. & Mackauer, M. (1995) Oviposition behavior of *Monoclonus paulensis* (Hymenoptera, Aphididae) – factors influencing reproductive allocation to hosts and host patches. *Annals of the Entomological Society of America*, **88**, 220–226.
- Minkenber, O.P.J.M., Tatar, M. & Rosenheim, J.A. (1992) Egg load as a major source of variability in insect foraging and oviposition behavior. *Oikos*, **65**.
- Olson, D.M. & Andow, D.A. (1998) Larval crowding and adult nutrition effects on longevity and fecundity of female *Trichogramma nubilale* Ertle & Davis (Hymenoptera: Trichogrammatidae). *Environmental Entomology*, **27**, 508–514.
- Olson, D.M., Fadamiro, H., Lundgren, J.G. & Heimpel, G.E. (2000) Effects of sugar feeding on carbohydrate and lipid metabolism in a parasitoid wasp. *Physiological Entomology*, **25**, 17–26.
- Rees, N.E. & Onsager, J.A. (1982) Influence of predators on the efficiency of the *Blaesoxipha* spp. parasites of the migratory grasshopper. *Environmental Entomology*, **11**, 426–428.
- Rosenheim, J.A. (1998) Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology*, **43**, 421–447.
- Rosenheim, J.A. & Rosen, D. (1991) Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: distinguishing the influences of egg load and experience. *Journal of Animal Ecology*, **60**, 83–893.
- SAS Institute (1995) JMP® Statistics and Graphics Guide, Version 3. SAS Institute Inc., Cary, USA.
- Schmale, I., Wäckers, F.L., Cardona, C. & Dorn, S. (2001) Control potential of three hymenopteran parasitoid species against the bean weevil in stored beans: the effect of adult parasitoid nutrition on longevity and progeny production. *Biological Control*, **21**, 134–139.
- Sholes, O.D.V. (1984) Responses of arthropods to the development of goldenrod inflorescences (Solidago: Asteraceae). *American Midland Naturalist*, **112**, 1–14.
- Siekmann, G., Tenhumberg, B. & Keller, M.A. (2001) Feeding and survival in parasitic wasps: sugar concentration and timing matter. *Oikos*, **95**, 425–430.
- Siro, E. & Bernstein, C. (1996) Time sharing between host searching and food searching in parasitoids: state-dependent optimal strategies. *Behavioral Ecology*, **7**, 189–194.
- Tylanakis, J.M., Didham, R.K. & Wratten, S.D. (2004) Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology*, **85**, 658–666.
- Wäckers, F.L. & Steppuhn, A. (2003) Characterizing nutritional state and food source use of parasitoids collected in fields with high and low nectar availability. *Proceedings of the IOBC/WPRS Study Group on Landscape Management for Functional Biodiversity, Bologna, Italy* (eds W.A. Rossing, H. Poehling & G. Burgio), pp. 203–208. International Organization of Biological Control.
- Winkler, K. (2005) *Assessing the Risks and Benefits of Flowering Field Edges*. PhD Thesis, Wageningen University, Wageningen.
- Winkler, K., Wäckers, F., Bukovinskine-Kiss, G. & van Lenteren, J. (2005) Sugar resources are vital for *Diadegma semiclausum* fecundity under field conditions. *Basic and Applied Ecology*, **115**, 187–194.
- Wyckhuys, K.A.G., Strange-George, J.E., Kulhanek, C.A., Wäckers, F.L. & Heimpel, G.E. (2008) Sugar feeding by the aphid parasitoid *Binodoxys communis*: how does honeydew compare to other sugar sources? *Journal of Insect Physiology*, doi: 10.1016/j.jinsphys.2007.11.007.

Received 18 June 2007; accepted 12 November 2007

Handling Editor: Jonathan Newman